

***Scytinopogon caulocystidiatus* and *S. foetidus* spp. nov., and five other species recorded from Brazil**

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ABSTRACT—Seven species of *Scytinopogon* in the Atlantic Forest of Brazil are described. *Scytinopogon caulocystidiatus* and *S. foetidus* are proposed as new species based on morphological and molecular data. Five other species are presented: *S. chartaceus*, *S. dealbatus* and *S. robustus*, originally described from Brazil; and *S. pallescens* and *S. scaber*, previously reported for Brazil. Illustrations of the basidiomata and microstructures, including SEM images of ornamented basidiospores, are provided for all taxa. Comparisons with morphologically similar taxa and a key to the seven species of *Scytinopogon* known to occur in Brazil are also presented.

KEY WORDS—coral fungi, *Hydnodontaceae*, neotropics, taxonomy, *Trechisporales*

Introduction

Scytinopogon Singer is a clavarioid genus that is mainly distributed in tropical and subtropical regions (García-Sandoval & al. 2004, Larsson & al. 2011). The genus comprises eight species (Corner 1970, Petersen 1988, Desjardin & Perry 2015) and is characterized by its light colored, densely branched basidiomata with flattened branches, monomitic hyphal system consisting of clamped, noninflated hyphae, usually 4-spored basidia, and slightly angular, hyaline basidiospores with verruculose-echinulate ornamentation (Corner 1950).

Scytinopogon was previously included in *Clavariaceae* Chevall. based on basidiome morphology (Corner 1950, 1970, García-Sandoval & al. 2004); however, it was also proposed as related to different taxa of *Hydnodontaceae* Jülich (Jülich 1981) or the “Thelephoroid” series (Corner 1950). The tough, coriaceous basidiomata in *Scytinopogon* support its removal from *Clavariaceae* (Jülich 1981); Larsson & al. (2011) and Birkebak & al. (2013) show a phylogenetic proximity of *Scytinopogon* to the corticioid genus *Trechispora* P. Karst. (*Trechisporales* K.H. Larss.). Morphological characters supporting the *Scytinopogon* + *Trechispora* clade are a monomitic hyphal system and clamped generative hyphae with subicular hyphae or context hyphae with ampulliform septa (Hibbett & al. 2007). The presence of calcium oxalate crystals is common in *Trechispora* but is a species-specific character (Jülich 1981). García-Sandoval & al. (2004) found these crystals in the basal mycelium hyphae of *Scytinopogon* species.

Reviews of previously reported species of *Scytinopogon* from Brazil were published by Corner (1953, 1966, 1970) for the Amazon and by Rick (1959, Rio Grande do Sul), Corner (1970, Rio de Janeiro), Petersen (1988, São Paulo), and Meijer (2006, 2008, Paraná) for the Atlantic Forest. These studies cited five species, but most lack complete descriptions.

Considering the wide distribution of *Scytinopogon* in tropical and subtropical regions, and with the goal of increasing what is known about the genus in the Atlantic Forest, this work provides detailed descriptions and illustrations of the seven *Scytinopogon* species recorded for Brazil: two new species (*S. caulocystidiatus*, *S. foetidus*); three species described first from Brazil (*S. chartaceus*, *S. dealbatus*, *S. robustus*); and two species originally described elsewhere (*S. pallescens*, *S. scaber*).

While this article was in preparation, Meiras-Ottoni & al. (2021) proposed synonymizing *Scytinopogon* under *Trechispora* based on ITS and 28S sequence analyses. Although we agree the two genera are phylogenetically related, we feel that additional DNA regions and species are needed before concluding that *Scytinopogon* and *Trechispora* are fully synonymous. We prefer to retain the present species in *Scytinopogon* until a more thorough revision of the group is conducted.

Material & methods

Morphological data

Field trips were conducted between January 2013 and August 2014 (with an additional expedition in January 2016) mostly during the rainy season in the states of

Rio Grande do Sul, São Paulo, and Santa Catarina. Whenever possible, macroscopic characters were studied from fresh specimens. Color codes (e.g., 2B19) are based on Kornerup & Wanscher (1978). Microscopic characters were observed from sections of dried basidiomata using an Olympus CX21 microscope and a 1000× immersion oil lens. Descriptive terms follow Corner (1947), Largent & al. (1977), and Vellinga & Noordeloos (2001). All microscopic structures were observed in water, 3% potassium hydroxide, Melzer's solution, and Congo red. Measurements were made in a solution of Congo red and 5% potassium hydroxide. Basidiospore measurements excluded ornamentation. At least twenty-five measurements were made of each microstructure. Q refers to the average basidiospore length/width ratio. The descriptions are based on all collections studied; the number of collections is shown in parentheses (s =) after each basidiospore measurement. Illustrations of microscopic features were based on digital photographs. Scanning electron microscopy (SEM) was conducted at the Laboratório Central de Microscopia Eletrônica (LCME/UFSC). Hymenophore fragments were removed from dried basidiomata, mounted on aluminum stubs using carbon adhesive tabs, coated with 30 nm of gold, and examined with a scanning electron microscope operating at 10 keV. Voucher material was deposited at the Universidade Federal de Santa Catarina, Florianópolis, Brazil (FLOR). The MATERIAL EXAMINED sections list specimens collected during the present work and the ADDITIONAL SPECIMENS EXAMINED were from BPI, CGE, FLOR, INPA, JPB, K, MBM, PACA, RBGE, and URM (Thiers 2017). The REFERENCE EXSICCATA STUDIED section lists specimens of other taxa that were used for taxonomic comparison.

Genomic DNA extraction, PCR and Sequencing

Genomic DNA was extracted from dried material using a PowerPlant®Pro DNA Isolation Kit, following the manufacturer's protocol adapted for fungi. The internal transcribed spacer of ribosomal nuclear DNA (nrITS) region was amplified using the primers ITS1F and ITS4R (Dentinger & al. 2010) and the following cycling parameters: an initial denaturation at 94°C for 2 min; 40 cycles of 30 s at 94°C, 45 s at 55°C and 1 min at 72°C; and a final extension at 72°C for 7 min. The PCR products were purified using PEG (polyethylene glycol; Sambrook & al. 1989). Sanger sequencing was performed with a BigDye Terminator 3.1 Cycle Sequencing Kit, following the manufacturer's protocol, using the same primers cited above, at Fundação Oswaldo Cruz (Fiocruz), Minas Gerais, Brazil. The generated sequences and their respective chromatograms were manually inspected and edited with Geneious v.6.1.8 (Kearse & al. 2012).

Phylogenetic analyses

Specimens and GenBank accession numbers used in this study are shown in TABLE 1. Newly generated DNA sequences were combined with the available ITS sequences of *Scytinopogon* from GenBank, as well as sequences of *Brevicellicium exile* (H.S. Jacks.) K.H. Larss. & Hjortstam and *Trechispora stellulata* (Bourdot & Galzin) Liberta as the outgroup, to construct a final 32-sequence matrix. Alignments were generated using

TABLE 1. *Scytinopogon* and outgroup sequences used in the phylogenetic analyses.
Newly generated sequences are set in bold font.

TAXON	VOUCHER	ORIGIN	GENBANK ACCESSION NUMBER
<i>S. caulocystidiatus</i>	FLOR 56314	Brazil	MK458772
<i>S. chartaceus</i>	FLOR 56185	Brazil	MK458775
<i>S. dealbatus</i>	FLOR 56182	Brazil	MK458776
	FLOR 56183	Brazil	MK458777
<i>S. foetidus</i>	FLOR 56315	Brazil	MK458769
<i>S. havencampii</i>	SFSUDED8300	São Tomé & Príncipe	KT253946
<i>S. pallescens</i>	FLOR 56184	Brazil	MK458767
	FLOR 56186	Brazil	MK458766
	FLOR 56187	Brazil	MK458771
	FLOR 56188	Brazil	MK458774
<i>S. robustus</i>	FLOR 56179	Brazil	MK458770
	FLOR 56190	Brazil	MK458768
<i>S. scaber</i>	FLOR 56189	Brazil	MK458773
<i>Scytinopogon</i> sp.	BAB5120	India	KT804576
	9P829	Taiwan	KF6795001
	0906RK610	Taiwan	KF6795051
	9P615	Taiwan	KF679498
	0906RK623	Taiwan	KF6795031
	9P1233	Taiwan	KF6795011
	0906RK71	Taiwan	KF6795021
	0906RK1023	Taiwan	KF6795061
	0906RK647	Taiwan	KF6795041
	9P79	Taiwan	KF6794991
<i>Scytinopogon</i> sp. 1	MEL2382623	Australia	KP012986
	MEL2382744	Australia	KP012927
	MEL2382716	Australia	KP012897
	MEL2382612	Australia	KP012977
<i>Scytinopogon</i> sp. 2	MEL2382992	Australia	KP012847
	MEL2382675	Australia	KP013038
	MEL2382987	Australia	KP012842
<i>Brevicellicium exile</i>	UV2022824	USA	KP814539
<i>Trechispora stellulata</i>	UC2022931	USA	KP814168

MAFFT v. 7 (Katoh & Standley 2013) according to E-INS-i criteria. Sequences were then manually corrected using the software MEGA v.7.0.14 (Tamura & al. 2013). Indels present in the nrITS datasets were recoded as binary characters following the “simple indel coding method” (SIC, Simmons & Ochoterena 2000), which was implemented in SeqState (Müller 2005). The resulting binary characters were joined in the final matrix as a distinct partition. The final alignments (as well the final topologies) were logged in TreeBase (<http://purl.org/phylo/treebase/phylovs/study/TB2:S22377>). New sequences generated for this work were uploaded to GenBank (Sayers & al. 2009).

Maximum likelihood (ML) and Bayesian inference (BI) criteria were applied to the datasets, which were divided in three partitions for the ITS (ITS1/2, 5.8S and recoded indels). The best model of nucleotide evolution for each nucleotide partition was determined using BIC (Bayesian information criterion) with the software jModelTest v2.1.6 (Guindon & Gascuel 2003, Darriba & al. 2012). ML analyses were performed using the software RAXML v. 8.2.10 (Stamatakis 2014) available on the CIPRES portal (Miller & al. 2010, <http://www.phylo.org/>). The analysis first involved 100 ML searches, each starting from one randomized stepwise addition parsimony tree (command `-f d`), under a GTRGAMMA model, with all other parameters estimated by the software. To assess the reliability of the nodes, nonparametric bootstrapping replicates under the same model were computed, allowing the program to halt bootstrapping automatically with the autoMRE bootstrapping criterion. To plot the calculated bootstrap values on the branches, the command `-fb` was used. The BI was performed with the software Mr. Bayes v.3.2.6 (Ronquist & Huelsenbeck 2003), implemented in CIPRES Science Gateway 3.1. BI was performed using two independent runs, each starting from random trees, with four simultaneous independent chains, and performed 10,000,000 generations, keeping one tree every 1000th generation. Four rate categories were used to approximate the gamma distribution. Of all trees sampled, 20% were discarded as burn-in and checked by the convergence criterion (frequencies of average standard deviation of split <0.01) with Tracer v.1.6 (Rambaut & al. 2014), while the remaining were used to reconstruct a 50% majority-rule consensus tree and to estimate Bayesian posterior probabilities (BPP) of the branches. A node was considered strongly supported if it had a BPP ≥ 0.95 and/or BS $\geq 90\%$ and moderately supported if it had a BPP ≥ 0.90 and/or BS $\geq 70\%$.

Phylogenetic results

Twelve new nrITS sequences from *Scytinopogon* were generated during this study. The best models of nucleotide substitution estimated for the partitions were TPM2uf+G for the combined ITS1/ITS2 and K80 for the 5.8s. The recovered tree topologies resulting from both routines were basically identical. This work shows the topology from the ML analyses, with both BPP and BS values (FIG. 1). *Scytinopogon scaber*, *S. caulocystidiatus* and *S. dealbatus* are early branches in the trees. Four other clades are formed by the remaining species.

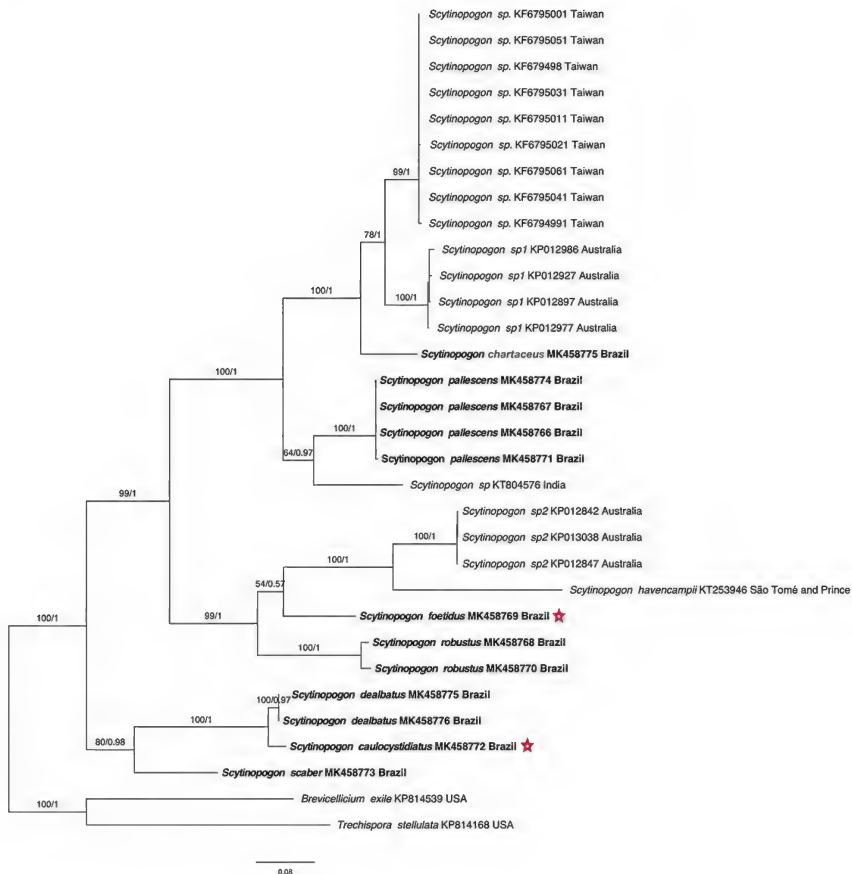


Fig. 1. Consensus tree from Maximum likelihood (ML) analysis of *Scytinopogon* based on a dataset of 32 nrITS sequences rooted with the outgroup (*Brevicellium exile* and *Trechispora stellulata*). Bayesian posterior probability (on the right of the “/”) >0.7 and bootstrap values (on the left of the “/”) >50% are shown. The twelve new sequences are highlighted in bold type. Red stars indicate the new taxa, *Scytinopogon caulocystidiatus* and *S. foetidus*.

In the analysis, the *Scytinopogon caulocystidiatus* sequence (FLOR 56314) is closely related to *S. dealbatus* (FLOR 56182, FLOR 56183) from Brazil (BS = 80, BPP = 0.98). Our molecular phylogeny (Fig. 1) confirms our morphological analyses that *S. caulocystidiatus* and *S. dealbatus* are distinct taxa.

Two *Scytinopogon robustus* sequences (FLOR 56190, FLOR 56179) clustered in a well-supported clade (BS = 99, BPP = 1) with the sequences

of *Scytinopogon foetidus*, *S. havencampii* (SSFU DEB8300) from São Tomé and Príncipe, and *Scytinopogon* sp. 2 from Australia.

The *Scytinopogon foetidus* sequence clustered in a weakly supported but resolved clade (BS = 54, BPP = 0.57) close to *S. havencampii* (SSFU DEB8300), suggesting that they are different species. This is supported by the morphological analysis, as discussed below.

The Brazilian *S. pallescens* sequences (FLOR 56184, FLOR 56186, FLOR 56187, FLOR 56188) clustered (BS = 64; BPP = 0.97) in a clade that included *Scytinopogon* sp. (BAB5120) from India. The clade including *Scytinopogon chartaceus* was strongly supported (BS = 100; BPP = 1). Sequences from *Scytinopogon* sp. (9P829, 0906RK610, 9P615, 0906RK623, 9P1233, 0906RK71, 0906RK1023, 0906RK647, 9P79) from Taiwan and *Scytinopogon* sp. 1 (MEL2382623, MEL2382744, MEL2382716, MEL2382612) from Australia were recovered as sister taxa of *S. chartaceus*.

Taxonomy

Scytinopogon caulocystidiatus A.N.M. Furtado & M.A. Neves, sp. nov. FIG. 2
MB 829606

Differs from *Scytinopogon dealbatus* by the presence of catenulate caulocystidia.

TYPE—Brazil. Santa Catarina: Florianópolis, Ilha do Campeche, Trilha do Morcego, 27°40'40"S 48°28'6"W, 24 III 2014, A.N.M. Furtado 460 (Holotype, FLOR 56314; GenBank 458772).

ETYMOLOGY—The epithet refers to the abundant catenulate caulocystidia.

BASIDIOMATA 35–70 mm tall, solitary, gregarious to densely caespitose, white (1A1), drying yellowish white (4A2) with reddish-brown (8D7) apices; branches subcylindric at first, becoming flattened, twisted, slightly subpruinose, 3.0 mm wide in the lower branches, tapering towards the apex, polychotomous below, di- or trichotomous towards the apex, branched three to five times, internodes gradually becoming smaller, apices subfusiform, acute, subterete, narrowly spathulate; STIPE cylindric, short, 10–20 × 3.0–5.0 mm. CONTEXT reddish brown (8DF), tough at stipe base; odor of ammonia; taste unrecorded.

BASIDIOSPORES 3.5–4.5 × 3.0–3.5 µm (Q = 1.06) (s = 2 specimens), subglobose, hyaline, uniguttulate, slightly angular, with diminutive spines, ≤0.5 µm long, slightly thick-walled, apex blunt, inamyloid; hilar appendage ≤0.5 µm. BASIDIA 20–29 × 4.5–6.0 µm, clavate, clamped; 2- or 4-spored, 3.5–5.0 µm long. CYSTIDIA in stipitipellis as caulocystidial hairs, 58–72 ×

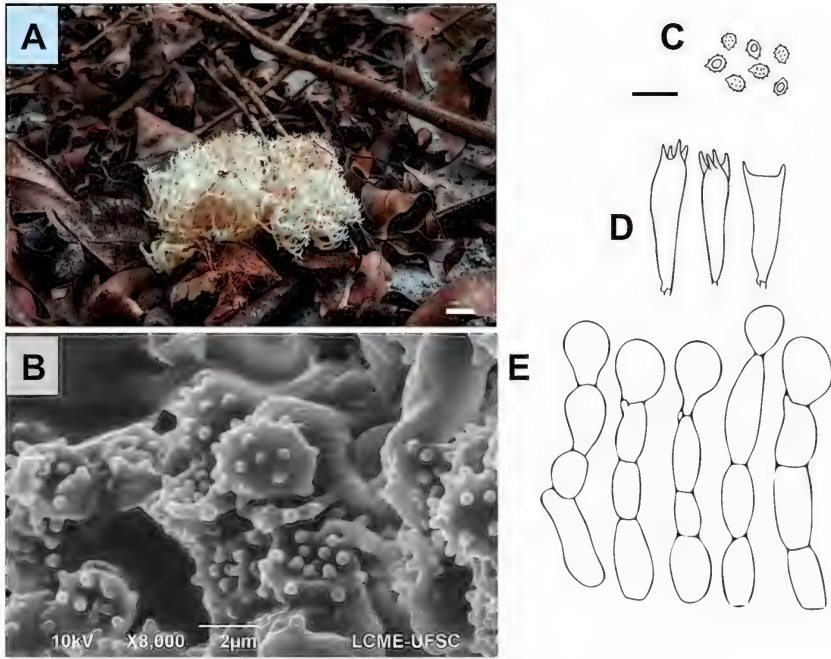


FIG. 2. *Scytinopogon caulocystidiatus* (FLOR 56314). A. Fresh basidiomata in situ; B, C. Basidiospores; D, Basidia; E. Capitulate cystidial hairs of stipitipellis. Scale bars: A = 1 cm; C–E = 10 µm.

10–18 µm, formed by concatenation of narrowly utriform, capitate to sphaeropedunculate hyphae, smooth, thin-walled, clamped; peduncle when present 4.0×2.0 µm. HYMENIUM ≤ 62.5 µm thick, thickening upward, amphigenous, stratified into three layers, older basidia tortuous to collapsed, absent in stipe. SUBHYMENIUM ≤ 40 µm thick, constricted at the septa, hyphae 5.0 µm diam, thin-walled. CONTEXT with subparallel arranged hyphae 4.0–6.0 µm diam, cylindric, alternating with inflated hyphae 10–12 µm wide, ampulliform segments rare, 6.0–7.0 µm wide, thin-walled, clamped. Internal stipe hyphae 2.0–7.0 µm diam, irregularly inflated, pale yellow (1A2).

ECOLOGY & DISTRIBUTION—On sandy soil in forest on marine sands. Known only from the type locality.

ADDITIONAL MATERIAL EXAMINED—BRAZIL. SANTA CATARINA: Florianópolis, Unidade de Conservação Ambiental Desterro - UCAD, 27°31'50"S 48°30'44"W, 8 I 2016, M.L. Vanegas-León 61 (FLOR 59324).

COMMENTS—*Scytinopogon caulocystidiatus* is difficult to see in the field as its white basidiomata grow on a whitish, sandy substrate.

Scytinopogon caulocystidiatus and *S. dealbatus* have basidiomata that are the same size, shape, color, and consistency. Also, unlike most *Scytinopogon* species, both have an amphigenous hymenium. *Scytinopogon dealbatus* can be separated by its ellipsoid basidiospores and the absence of caulocystidia.

Besides the strong odor of ammonia, a diagnostic characteristic of this species is the cystidial stipitipellis, previously undescribed for *Scytinopogon* (Corner 1950, 1970, Petersen 1988, García-Sandoval & al. 2004).

Scytinopogon chartaceus (Pat.) R.H. Petersen, Mycologia 80: 574. 1988
[as 'chartaceum'].

FIG. 3

BASIDIOMATA 30–65 × 25–47 mm, solitary to gregarious, chalk-white (1A1), becoming grayish white (1B1), drying pale yellow (3A4), palmately forked from a flattened stipe immersed in soil, branching in a plane, twisted; branches flattened and narrowly spatulate, 2.0–6.0 mm wide in the lower branches, tapering towards the apex, polychotomous below, becoming

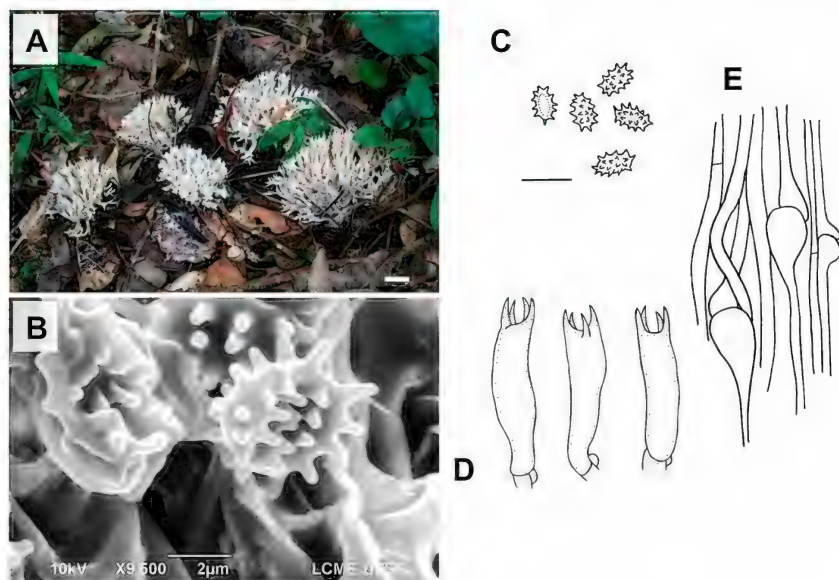


FIG. 3. *Scytinopogon chartaceus*. (FLOR 56185). A. Fresh basidiomata in situ; B, C. Basidiospores; D. Basidia; E. Context hyphae with ampulliform septa.

Scale bars: A = 1 cm; C–E = 10 µm.

dichotomous, branched two to four times, internodes diminishing gradually; axils U-shaped, apices acute to blunt, subterete, suede-like above, smooth below; STIPE 15–30 × 7.0–15 mm, sometimes branched from the base, dilated and flattened below the branching points, arising from very scarce white mycelial strands on the soil. CONTEXT pale yellow (1A2), waxy, tough at the base of the stipe, drying cartilaginous; odor and taste unrecorded.

BASIDIOSPORES 6.0–8.0 × 3.0–4.5 μm ($Q = 1.82$) ($s = 1$ specimen), narrowly ellipsoid, hyaline, angular-echinulate, slightly thick-walled, spines 0.7–1.5 μm long, apex blunt, inamyloid; hilar appendage obscured by spore ornamentation. BASIDIA 25–32 × 6.0–8.0 μm , clavate, barrel-shaped, with homogeneous to minutely guttulate contents, clamped; 1–2-spored, 4.0–7.0 μm long. CYSTIDIA absent. HYMENIUM thickening upward, ≤ 100 μm thick, covering the undersides of the branches. SUBHYMENIUM c, 30 μm thick, hyphae 2.5–3.0 μm diam, thin-walled. CONTEXT with parallel arranged hyphae 3.5–4.0 μm diam, cylindric and long-celled, slightly thick-walled, ampulliform septa 5.5–8.0 μm diam, clamped. Surface of sterile base composed of repent hyphae 2.5–5.0 μm wide, smooth, thin-walled, clamped. Irregular crystals of calcium oxalate covering the contextual and basal mycelium hyphae.

ECOLOGY & DISTRIBUTION—On soil among litter, in Atlantic Forest. Known only from São Paulo (Campinas, Patouillard 1907; São Paulo, Petersen 1988), and Santa Catarina (present study), Brazil.

MATERIAL EXAMINED—BRAZIL. SANTA CATARINA: Florianópolis, Trilha para Naufragados, 27°49'4"S 48°33'37"W, 23 V 2014, A.N.M. Furtado 504 (FLOR 56185; GenBank MK 458775).

COMMENTS—The Brazilian type specimen, published as *Lachnocladium chartaceum* by Patouillard (1907), was not studied due to its poor condition. The identification of the specimen from Santa Catarina was based on the original protologue (Patouillard 1907) and the description of a specimen collected by Leif Ryvarden in São Paulo, Brazil, and identified as *S. chartaceus* by Petersen (1988).

Morphologically, *S. pallescens* is the most similar species; however, *S. pallescens* has larger internodes on its branches, the surface of the basidiomata is rugulose and subtomentose, and the well-developed basal mycelium is very compact (Corner 1950, 1970, Petersen 1988). *Scytinopogon chartaceus* has smaller internodes, basidiomata with a smooth surface, and scarce and loosely attached basal mycelium (Petersen 1984). Also, *S. pallescens* has nodulose to verrucose basidiospores and *S. chartaceus* has echinulate basidiospores with long spines (Reid 1962, Petersen 1988).

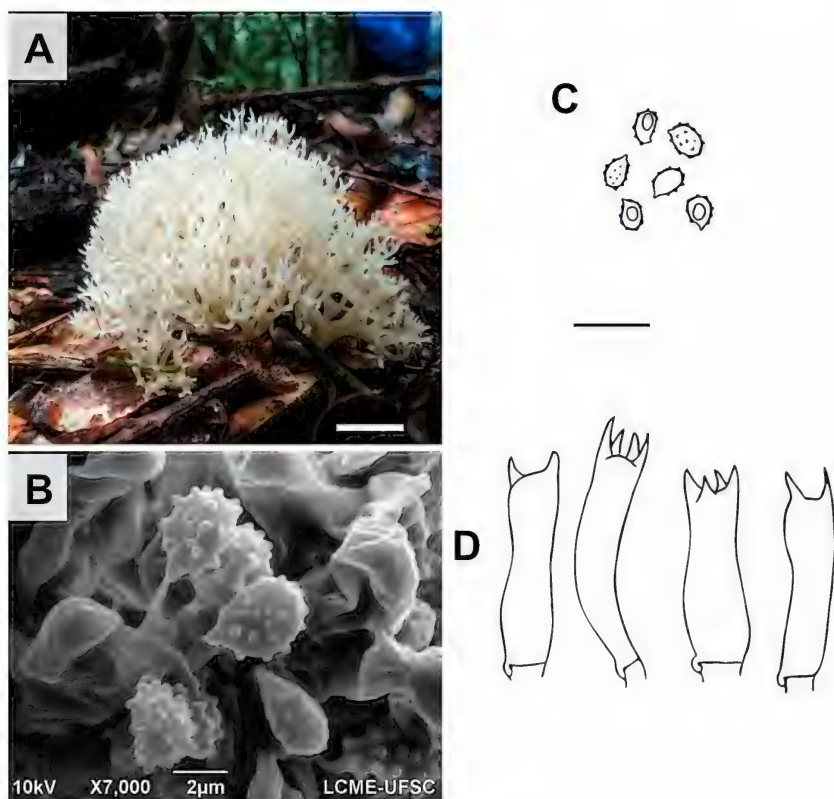


FIG. 4. *Scytinopogon dealbatus*. (FLOR 56183). A. Fresh basidiomata in situ; B, C. Basidiospores; D. Basidia. Scale bars: A = 1 cm; C–D = 10 μm.

Scytinopogon dealbatus (Berk.) Corner,
Beih. Nova Hedwigia 33: 89. 1970.

FIG. 4

BASIDIOMATA 55–75 mm tall, solitary to gregarious, white (1A1), the hymenium becoming pale yellow (1B3), drying to reddish brown (5C4); branching often polychotomous from the base, becoming dichotomous above, branched three to four times; branches 1.0–3.0 mm thick, ligulate, smooth; axils flat; apices concolorous with branches; STIPE 2.0–3.0 mm thick, slightly distinct, white (1A1). CONTEXT gelatinous; taste and odor unrecorded.

BASIDIOSPORES 4.0–4.5 × 2.5–3.5 μm ($Q = 1.39$) ($s = 2$ specimens), ellipsoid, hyaline, echinulate to almost spineless, uniguttulate, warts ≤0.4 μm long, inamyloid; hilar appendage ≤1.0 μm, often sublateral. BASIDIA 21–29 × 5.0–7.0 μm, clavate, clamped; (2–)4-spored, 3.5–6.0 μm long. CYSTIDIA

absent. HYMENIUM ≤ 150 μm thick, thickening upward, amphigenous, absent in stipe. SUBHYMENIUM ≤ 20 μm thick, composed of loosely interwoven hyphae ≤ 5.0 μm diam, thin-walled. CONTEXT hyphae subparallel, slightly agglutinated, 5.0–6.5 μm diam, walls thin, subgelatinous; ampulliform septa 6.6–13 μm diam, clamped.

ECOLOGY & DISTRIBUTION—In the Atlantic Forest, this species is found on soil. In Brazil, it is known from Amazonas (type locality), Mato Grosso (Corner 1970), Paraná (Meijer 2006), São Paulo (Petersen 1988) and Rio Grande do Sul (Rick 1959; present study). It is also recorded for Bolivia, Panama (Corner 1970), and Venezuela (Petersen 1988).

MATERIAL EXAMINED—BRAZIL. RIO GRANDE DO SUL: Porto Alegre, Universidade Federal do Rio Grande do Sul, Campus do Vale, 30°04'23.8"S 51°07'23.6"W, 1 IV 2014, E.P. Fazolino 176 (FLOR 56182; GenBank MK458776), E.P. Fazolino 177 (FLOR 56183, GenBank MK458777).

ADDITIONAL SPECIMENS EXAMINED—BRAZIL. RIO GRANDE DO SUL: Panurê, São Jerônimo, 1873, Spruce s.n. (K 135803, 135804, holotype of *Clavaria dealbata* Berk.); São Leopoldo, 1904, J.E. Rick s.n. (BPI 295129; PACA 17230, 17241, 17246, 17251, as *Lachnocladium dubiosum*); 1907, J.E. Rick s.n. (BPI 295385, 333169, 333170, 333171 as *Scytinopogon dubiosum* ad. int.); 1932, J.E. Rick s.n. (BPI 295383). MATO GROSSO: Chavantina, 1 II 1968, E.J.H. Corner s.n. (RBGE 101765).

COMMENTS—*Scytinopogon dealbatus* basidiomata resemble young *Scytinopogon scaber* but lack the erect habit and papillate branches (Petersen 1988). Also, the hymenium is present on both sides of the branches, contrary to other *Scytinopogon* species where the hymenium is unilateral. The gelatinous context is only known to occur in *S. dealbatus*. This character is rather common in *Ramaria* species; however, it is rarely reported in *Scytinopogon* (Petersen 1988).

Scytinopogon pallescens could be mistaken for a robust form of *S. dealbatus*. However, *S. pallescens* has flattened branches with the hymenium on one side of the branches, mycelia at the base of the stipe, angular-nodulose basidiospores, and lacks a gelatinous context (Corner 1950).

Petersen (1984, 1988) proposed transferring *S. dealbatus* to *Ramariopsis* based on the gelatinous context of the fresh basidiomata (a character never reported for *Scytinopogon*) and the ellipsoid and echinulate basidiospores rather than angular-nodulose basidiospores described by Corner (1970). However, Petersen (1988), who also studied a specimen from Venezuela collected by Roy Halling and identified as *S. dealbatus*, agreed that the species shares more characters with *Scytinopogon* than with *Ramariopsis*, especially because *S. dealbatus* lacks the dextrinoid reaction characteristic of *Ramariopsis* and not found in *Scytinopogon*.

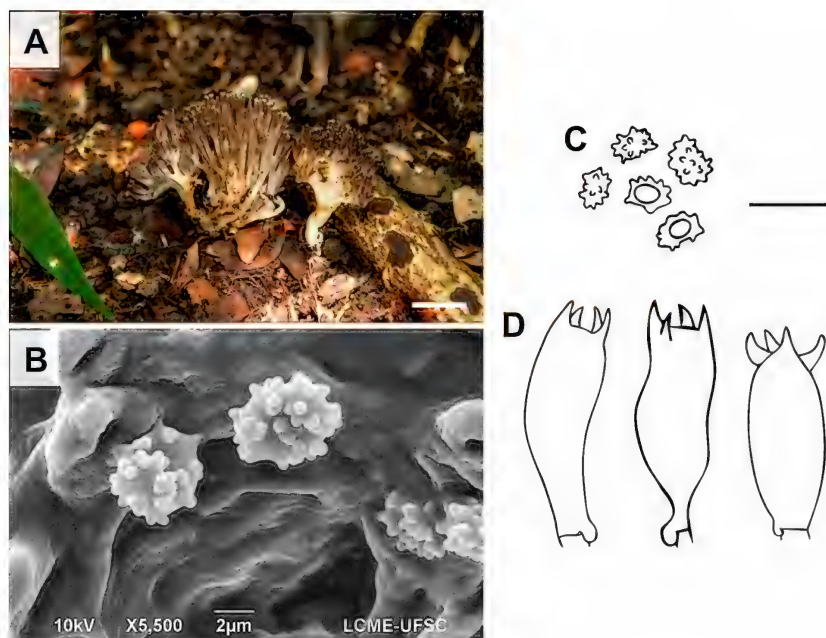


FIG. 5. *Scytinopogon foetidus*. (FLOR 56315).

A. Fresh basidiomata in situ; B, C. Basidiospores; D. Basidia.

Scale bars: A = 1 cm; C–D = 10 μ m.

***Scytinopogon foetidus* A.N.M. Furtado & M.A. Neves, sp. nov.**

FIG. 5

MB 829605

Differs from *Scytinopogon havencampii* by its 4-spored basidia, its slightly concave ellipsoid basidiospores, its ampulliform septa, its strong putrid odor, and by the presence of calcium oxalate crystals.

TYPE—Brazil. Santa Catarina: Florianópolis, Costão do Santinho, Morro das Aranhas, 27°47'66"S 48°38'18"W, 27 I 2014, A.N.M. Furtado 423 (**Holotype**, FLOR 56315; GenBank MK458769).

ETYMOLOGY—The epithet refers to the strong, unpleasant odor of the fresh basidiomata.

BASIDIOMATA 25–55 mm tall, gregarious, pale grayish beige (4C2), becoming reddish brown (8E6) to deep brown (8F5) upward, the apices pure white (1A1), palmately branched from a flattened stipe, branching in one plane, sometimes twisted, subpruinose; branches cylindric to flattened and narrowly spathulate, 3.0–4.0 mm wide in the lower branches, tapering

towards the apex, polychotomous below, becoming dichotomous, branched three to four times, narrowly U-shaped, flattened below the branching points, internodes gradually becoming smaller, apices blunt, subterete, narrowly ligulate; STIPE 8.0–15 × 2.0–6.0 mm, rarely branched from the base, pale grayish beige (4C2). CONTEXT pale yellow (1A2), slightly viscid, tough at the base of the stipe; odor strong and putrid; taste unrecorded.

BASIDIOSPORES 5.0–6.5 × 3.0–4.0 µm ($Q = 1.52$) ($s = 1$ specimen), ellipsoid, the inner side slightly applanate to slightly concave, hyaline, finely verrucose, thin-walled, warts 0.4–0.6 µm long, apex blunt, inamyloid; hilar appendage small. BASIDIA 23–28 × 7.0–9.0 µm, clavate, barrel-shaped, clamped; 4-spored, 3.0–5.0 µm long. CYSTIDIA absent. HYMENIUM ≤32.5 µm thick, absent in stipe. SUBHYMENIUM ≤50 µm thick, with loosely interwoven hyphae, 3.5–5.0 µm diam, thin-walled. CONTEXT with subparallel arranged hyphae 3.5–8.0 µm diam, thin-walled, constricted at the septa, ampulliform septa 5.0–6.0 µm diam, clamped. Surface of stipe composed by a trichodermal pellis, with cylindric hyphae up to 3.0 µm diam, slightly thick-walled, clamped. Crystals of calcium oxalate in needle clusters covering the cortical hyphae from the stipe.

ECOLOGY & DISTRIBUTION—On soil in forest, perhaps also lignicolous. Known only from the type locality.

COMMENTS—Given that many basidiomata in *Scytinopogon* are white, *S. foetidus* and *S. robustus* appear similar in their grayish-purple coloration. *Scytinopogon robustus*, however, is slenderer and drier, with flattened branches and a unilateral hymenium (Corner 1970). It also has inflated hyphae and lacks the putrid odor and the calcium oxalate crystals in the stipe cortex.

Another pigmented species, *S. havencampii* Desjardin & B.A. Perry, described from Príncipe Island, Africa, differs in its cylindric, orangish-white stipe, 2-spored basidia with long sterigmata, ellipsoid, nonconcave basidiospores, indistinct odor, and absence of ampulliform septa and calcium oxalate crystals (Desjardin & Perry 2015). The molecular phylogeny also supports *S. foetidus* and *S. havencampii* as distinct species, but closely related species and in the same clade (FIG. 1).

Another pigmented species, *Scytinopogon echinosporus* (Berk. & Broome) Corner, known from Sri Lanka and Java, differs in its pale purple, often flattened branches with dark violet-brown tips, ellipsoid to angular basidiospores, 4-spored basidia, and inflated (≤12 µm diam) hyphae.

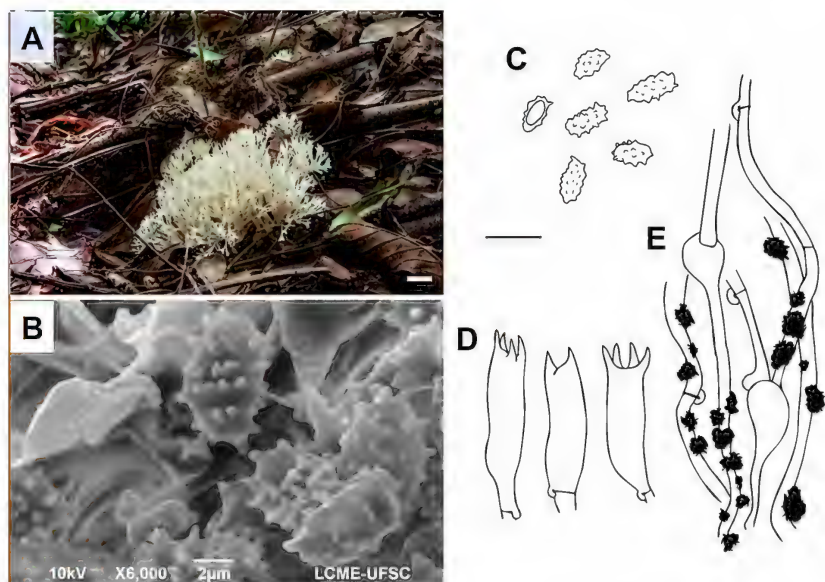


FIG. 6. *Scytinopogon pallescens*. (FLOR 56184). A. Fresh basidiomata in situ; B, C. Basidiospores; D. Basidia; E. Context hyphae with ampulliform septa. Scale bars: A = 1 cm; C–E = 10 µm.

Scytinopogon pallescens (Bres.) Singer, Lloydia 8(3): 139. 1945.

FIG. 6

BASIDIOMATA 40–110 mm tall, solitary, gregarious or densely caespitose, chalk-white (1A1) when young, pale yellow (1A2) in age, not changing when dried, palmately branched from a flattened stipe immersed in the soil, branching four to six times in one plane but twisted; branches slightly rugulose, flattened and narrowly spathulate, the upper side of the branches minutely subtomentose, 3.0–5.0 mm wide in the lower branches, tapering towards the apex, polychotomous below, becoming dichotomous, internodes becoming gradually longer; apices white (1A1), acute to blunt, subulate or subterete, narrowly ligulate; **STIPE** 15–45 × 2.0–4.0 mm, sometimes branched from the base, dilated and flattened below the branch nodes, arising from compact mycelial strands in the soil. **CONTEXT** pale yellow (1A2), slightly coriaceous, tough at the base of the stipe; odor unpleasant; taste unrecorded.

BASIDIOSPORES 6.0–7.5 × 3.0–4.5 µm ($Q = 1.96$) ($s = 5$ specimens), narrowly ellipsoid, hyaline, angular-nodulose, finely verrucose, slightly thick-walled, warts 0.3–0.6 µm long, apex blunt, inamyloid; hilar appendage small. **BASIDIA** 25–32 × 6.0–8.0 µm, clavate, finely granular-vacuolate, clamped; 2–4-spored, 4.0–5.0 µm long. **CYSTIDIA** absent. **HYMENIUM** ≤40 µm thick,

thickening upward, ≤ 250 μm thick, covering the underside of the branches. SUBHYMENIUM ca. 30 μm thick, composed of loosely interwoven hyphae, 2.5–5.0 μm diam, thin-walled. CONTEXT compact, with parallel arranged hyphae 3.5–4.0 μm diam, cylindric, with ampulliform septa 5.0–6.0 μm diam, slightly thick-walled, clamped. Surface of sterile base composed of a trichodermal pellis, hyphae 1.5–3.0 μm diam, smooth, thin-walled, clamped. Crystals of calcium oxalate in rosettes, covering the hyphae in the context and basal mycelium.

ECOLOGY & DISTRIBUTION—In the Atlantic Forest, this species is found on soil and is possibly lignicolous. In Brazil, it is known from Amazonas, Mato Grosso, Pará, Paraná, Rio de Janeiro, Rio Grande do Sul (Corner 1953, 1966, 1970; Meijer 2006) and Santa Catarina (present study). It is also known from Burma, Cameroon, Congo (type locality), Cuba, Japan, Java, Madagascar, Malaysia, Mauritius, Nigeria, Panama, Sumatra, the Philippines, Solomon Islands, Uganda, the USA (Corner 1950, 1966, 1970), and India (Thind 1961; Dutta & al. 2012).

MATERIAL EXAMINED—**BRAZIL. SANTA CATARINA:** Florianópolis, Lagoa do Peri, Trilha da Cachoeira, 27°74'41"S 48°52'04"W, 15 II 2014, A.N.M. Furtado 441 (FLOR 56187; GenBank MK458771); 19 III 2014, A.C. Magnago 974 (FLOR 56186; GenBank MK458766); Universidade Federal de Santa Catarina, Campus Trindade, Depto de Botânica, 27°60'17"S 48°52'50"W, 26 III 2013, A.N.M. Furtado 304 (FLOR 56184; GenBank MK458767); 14 IV 2014, A.N.M. Furtado 488 (FLOR 56188; GenBank MK458774); M.A. Neves 588 (FLOR 56197).

ADDITIONAL SPECIMENS EXAMINED—**BELIZE**, 2002, P.J. Roberts s.n. (K 109202, 109203, 109237). **BRAZIL. PARAÍBA:** Mataraca, 06 VI 2011, F. Wartchow s.n. (JPB 45094). **PERNAMBUCO:** Recife, Parque Estadual de Dois Irmãos, 13 VIII 1954, O.S. Silva n.n. (URM 876); Vitória de Santo Antão, Itamatamirim, 17 IX 1954, S.J. Silva n.n. (URM 1071). **Rio Grande do Sul:** no location, 1925, J.E. Rick s.n. (BPI 295379, 333159, 333160, 333162, 333164, 723389, as *Clavaria pteruloides* Pat. & Gaillard), 1907, J.E. Rick s.n. (PACA 17243, as *Lachnocladium moelleri* Henn.); São Leopoldo, 1925, J.E. Rick s.n. (BPI 295379, 333159, 333160, 333162, 333164, 723389). **MALAYSIA. MALAYA:** Pahang, 25 XI 1930, E.J.H. Corner s.n. (BPI 295368).

COMMENTS—*Scytinopogon pallescens* is morphologically highly variable and a common species in tropical and subtropical regions (Corner 1970).

Scytinopogon pallescens is easily recognized macroscopically by its chalk-white basidiomata with flattened branches. Microscopically, it has hyaline ellipsoid, angular-echinulate basidiospores, and uninflated, non-mucilaginous hyphae throughout the basidioma (Corner 1950). Some of our collections had basidiospores with such subtle angles that they appeared ellipsoid. In addition, the specimens have chalk-white basal mycelia that divide palmately before reaching the surface of the substrate.

Corner (1970) referred many Brazilian collections to *Scytinopogon angulisporus* (Pat.) Corner, including several specimens from Rio Grande do Sul that Petersen (1984) redetermined as *S. pallescens*. *Scytinopogon angulisporus* is no longer accepted in *Scytinopogon*, since its type specimen is conspecific with *Clavulina connata* (Berk.) Corner (Petersen 1984).

Scytinopogon chartaceus is quite similar to *S. pallescens*, in both color and morphology of the basidioma; however, *S. chartaceus* has more strongly echinulate basidiospores. This ornamentation is unusual for most *Scytinopogon* species, which are normally nodulose-warted with cushion-shaped warts (Petersen 1988).

Scytinopogon robustus (Rick) Corner, Beih. Nova Hedwigia 33: 91. 1970. FIG. 7

BASIDIOMATA 23–35 mm tall, solitary or caespitose, pale grayish (19B2), drying pale yellow (3A4), subfragile, flattened; branches flattened to subcylindric, bifurcate with slightly compressed axils, branched three times, subacute, mostly dichotomous, internodes irregular, diminishing gradually towards the apex; apices grayish violet (15E5), subulate,

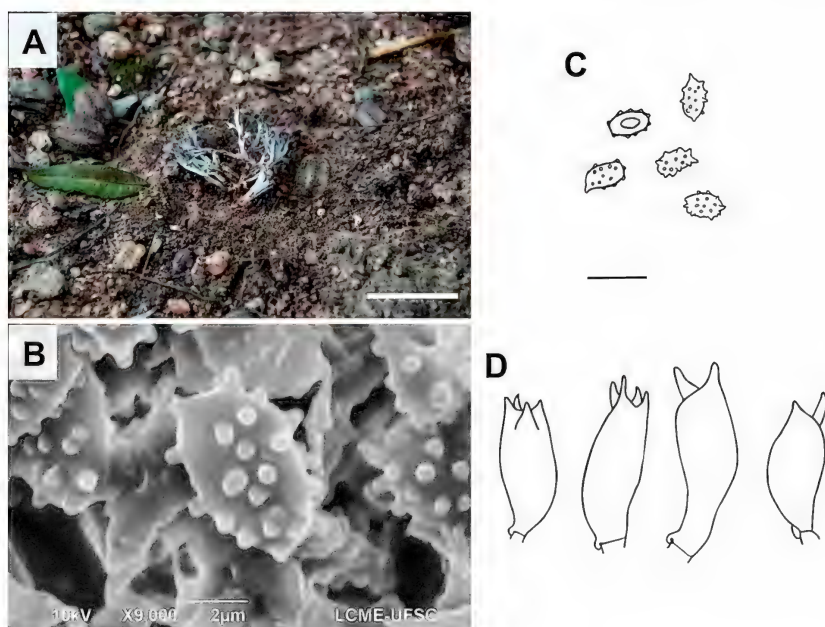


FIG. 7. *Scytinopogon robustus*. (FLOR 56190).

A. Fresh basidiomata in situ; B, C. Basidiospores; D. Basidia.

Scale bars: A = 1 cm; C–D = 10 µm.

sometimes blunt, subcristate to subpalmate; STIPE 9.0×2.0 mm, white to pale grayish (19B2), smooth, cylindric to flattened, coriaceous-fibrous. CONTEXT hollow; odor and taste not distinctive.

BASIDIOSPORES $6.0\text{--}6.5 \times 3.5\text{--}4.0$ μm ($Q = 1.53$) ($s = 3$ specimens), ellipsoid, hyaline, angular-nodular, slightly echinulate, slightly thick-walled, warts $0.4\text{--}0.8$ μm long, inamyloid; hilar appendage obscured by spore ornamentation. BASIDIA $22\text{--}31 \times 7.0\text{--}10$ μm , clavate, barrel-shaped, clamped; (2)4-spored, $3.0\text{--}5.0$ μm long, homogeneous to minutely guttulate. CYSTIDIA absent. HYMENIUM ≤ 37.5 μm thick, covering the undersides of the branches. SUBHYMENIUM c. 20 μm thick, hyphae $3.0\text{--}3.5$ μm diam, slightly inflated, clamped. CONTEXT with subparallel arranged hyphae $6.0\text{--}23$ μm diam, inflated, thin-walled, slightly constricted at the septa, clamped. Surface of sterile base covered by repent hyphae ≤ 3.0 μm diam, smooth, hyaline, clamped; medullary basal hyphae $12\text{--}15$ μm diam.

ECOLOGY & DISTRIBUTION—In the Atlantic Forest, *S. robustus* occurs on soil among litter. In Brazil, it is known from Paraná (Meijer 2006), Rio de Janeiro (Corner 1970), Rio Grande do Sul (type locality, Rick 1931, 1959), and Santa Catarina (present study). It is also known from Puerto Rico (Corner 1970) and Mexico (García-Sandoval & al. 2004).

SPECIMENS EXAMINED—BRAZIL. SANTA CATARINA: Florianópolis, Morro da Lagoa, Trilha do Jipe, $27^{\circ}59'43''\text{S}$ $49^{\circ}47'83''\text{W}$, 23 I 2013, A.N.M. Furtado 422 (FLOR 56190; GenBank MK548768); Costão do Santinho, Morro das Aranhas, $27^{\circ}47'66''\text{S}$ $48^{\circ}38'18''\text{W}$, 27 I 2014, A.N.M. Furtado 431 (FLOR 56179; GenBank MK458770). SÃO PAULO: Caraguatatuba, Serra do Mar, 19 I 2016, E.T.F. Linhares 144a (FLOR 59329).

ADDITIONAL SPECIMENS EXAMINED—BRAZIL. RIO GRANDE DO SUL: Pareí Novo, 1935, J.E. Rick s.n. (PACA 12457, holotype).

COMMENTS—Although our collection is small in size and has fragile basidiomata, *Scytinopogon robustus* can reach $50\text{--}100$ mm tall (Rick 1931, García-Sandoval & al. 2004). However, the epithet refers to the size of the basidiospores, which are larger than the spores of other *Scytinopogon* species.

Scytinopogon pallescens, a widespread species, looks like a pale form of *S. robustus*; however, *S. pallescens* has larger basidiospores ($5.5\text{--}7.0 \times 3.5\text{--}4.0$ μm) and its hyphae are not inflated (occasionally ≤ 10 μm diam) (Corner 1950, 1970, García-Sandoval & al. 2004).

Among the known species of *Scytinopogon*, only *S. robustus* and *S. echinosporus* have inflated hyphae (Corner 1970). *Scytinopogon echinosporus* has basidiomata with light brown apices and smaller basidiospores ($4.5\text{--}5.5 \times 3.5$ μm , García-Sandoval & al. 2004).

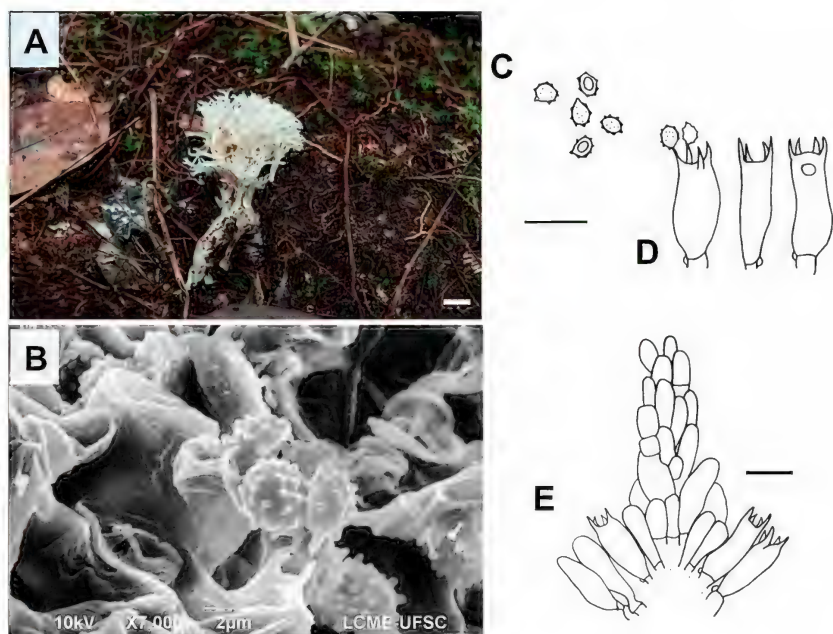


FIG. 8. *Scytinopogon scaber*. (FLOR 56189). A. Fresh basidiomata in situ; B, C. Basidiospores; D. Basidia; E. Context hyphae with ampulliform septa. Scale bars: A = 1 cm; C–E = 10 μm.

Scytinopogon scaber (Berk. & M.A. Curtis) D.A. Reid,
Persoonia 2(2): 161. 1962.

FIG. 8

BASIDIOMATA 95 mm tall, solitary to scattered, white (1A1), slightly translucent to slightly pinkish close to the stipe, the apices concolor, branched; branches in one plane, becoming inclined and horizontal, flattened and narrowly spatulate, polychotomous below, becoming dichotomous, internodes spaced, subterete, slightly expanded at the axils, the underside developing minute spines or papillae (these scattered at first, then crowded and concrescent), entire or slightly dentate, irregular, apices ligulate; **STIPE** 35 × 7.0 mm, dilating 3.0 mm wide upward. **CONTEXT** rather dry, firm; odor and taste absent.

BASIDIOSPORES 3.0–4.0 × 2.5–3.5 μm ($Q = 1.26$) ($s = 1$ specimen), broadly ellipsoid, hyaline, slightly angular, echinulate, warts 0.2–0.5 μm long, inamyloid; hilar appendage obscured by spore ornamentation. **BASIDIA** 15–18 × 4.5–5.5 μm, clavate, finely granular-vacuolate, clamped; 4-spored, 2.0–4.0 μm long. **CYSTIDIA** absent. **HYMENIUM** ≤20 μm thick, thickening

upward, amphigenous, covering the undersides of the branches, sterile on the hypogenous region. SUBHYMENIUM $\leq 15 \mu\text{m}$ thick, hyphae $2.5\text{--}5.0 \mu\text{m}$ diam, thin-walled. CONTEXT with parallel arranged hyphae $3.5\text{--}4.0 \mu\text{m}$ diam, cylindric, slightly thick-walled, inner hyphae $8.0\text{--}12 \mu\text{m}$ diam, not inflated, clamped. Surface of sterile base with cylindric repent hyphae $3.0 \mu\text{m}$ diam, disarticulated, slightly thick-walled.

ECOLOGY & DISTRIBUTION—In the Atlantic Forest, this species occurs on soil. It was previously reported for Brazil (without any details of localities or specimens) by Corner (1970), and here we record it for Santa Catarina. It is also known from Fiji (type locality), Brunei (Corner 1970), and Mexico (Ramírez-Lopes & al. 2012).

MATERIAL EXAMINED—BRAZIL. SANTA CATARINA: Santo Amaro da Imperatriz, Hotel Plaza Caldas da Imperatriz, Trilha da Pousada, $27^{\circ}70'39''\text{S}$, $48^{\circ}80'37''\text{W}$, 10 IV 2014, A.N.M. Furtado 483 (FLOR 56189; GenBank MK548773).

ADDITIONAL SPECIMENS EXAMINED—BRUNEI. 1959, E.J.H. Corner s.n. (K 69072), 1992, B.M. Spooner s.n. (K 27130).

COMMENTS—Originally described from Fiji, *Scytinopogon scaber* is diagnosed by its small, echinulate basidiospores and branched, clavarioid, distinctly papillate basidiomata (Ramírez-Lopes & al. 2012).

The collection from Santa Catarina is quite similar to Corner's collection from Brunei, except for some hyphae in the context that are broader in the Brazilian specimen ($2.0\text{--}3.5 \mu\text{m}$ diam on Corner's specimen).

Scytinopogon papillosus Corner, the only other *Scytinopogon* species with a papillate hymenophore (Corner 1970), can be distinguished by its reddish basidiomata, very strongly inflated hyphae ($3.0\text{--}25\text{--}[30] \mu\text{m}$ diam), and larger ($4.0\text{--}4.5 \times 2.7\text{--}3.5 \mu\text{m}$) ellipsoid basidiospores (Corner 1970). *Scytinopogon papillosus* is known only from Bolivia, from Singer's collection in Corner (1970). Unfortunately, the type collection was not found so our comparison was based on Corner's protologue.

Key to *Scytinopogon* species in Brazil

1. Hymenophore becoming more or less minutely papillate or hydroid *S. scaber*
1. Hymenophore smooth 2
2. Basidiomata light brown to reddish brown when fresh 3
2. Basidiomata pure white to pale yellow when fresh 4
3. Basidiomata slender with flattened branches,
context dry; context hyphae inflated to $6.0\text{--}23 \mu\text{m}$ diam *S. robustus*
3. Basidiomata robust with cylindric to flattened and narrowly spatulate branches,
context viscid; context hyphae $3.5\text{--}8 \mu\text{m}$ diam *S. foetidus*

- 4. Basidiomata subfragile, reddish brown when dry; basal mycelium absent 5
- 4. Basidiomata more robust, pale yellow when dry; basal mycelium present 6
- 5. Basidiospores subglobose; cystidial hairs on stipitipellis *S. caulocystidiatus*
- 5. Basidiospores ellipsoid; no cystidial hairs on stipitipellis *S. dealbatus*
- 6. Basal mycelium abundant and very compact, crystals present, insoluble in KOH;
basidiospores nodulose, finely verrucose *S. pallescens*
- 6. Basal mycelium scant and loosely attached, crystals absent;
basidiospores truly echinulate *S. chartaceus*

REFERENCE EXSICCATA STUDIED—*Scytinopogon echinosporus*: SOLOMON ISLANDS. 1967. E.J.H. Corner s.n. (RBGE 101775). INDONESIA. 1996, R.F. Ellen s.n. (K 45815).

Scytinopogon papillosus: BOLIVIA. 17 III 1956, R. Singer B 2100, B 2100 A (CGE, holotype).

Discussion

The Brazilian Atlantic Forest harbors a great diversity of macrofungi and the continual description of new species in this area emphasizes the importance of studying and preserving this biome. This work expands what is known about clavarioid fungi in the Atlantic Forest by providing detailed descriptions and illustrations for seven *Scytinopogon* species and adding two new species. to both the region and the world.

This work also presents a more robust phylogeny for *Scytinopogon* generated from nrITS sequences of six out of eight known species, supporting *Scytinopogon caulocystidiatus* and *S. foetidus* as new, independent species and confirming the morphological differences between them and the rest of the genus.

Scytinopogon was historically classified in *Clavariaceae*, despite the proposed relationship with *Hydnodontaceae* and thelephoroid fungi. However, the results obtained by Larsson & al. (2011) and Birkebak & al. (2013) indicate *Scytinopogon* is related to *Trechispora*. Nevertheless, to clarify the classification of *Scytinopogon* in *Hydnodontaceae* (*Trechisporales*), a more comprehensive study with more samples and more molecular markers is needed.

We have also shown that despite its being rarely documented, *Scytinopogon* is both abundant and widespread in the tropics and subtropics.

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Literature cited

- Birkebak JM, Mayor JR, Ryberg KM, Matheny PB. 2013. A systematic morphological and ecological overview of the *Clavariaceae* (Agaricales). *Mycologia* 105(4): 896–911. <https://doi.org/10.3852/12-070>
- Corner EJH. 1947. Variation in the size and shape of spores, basidia and cystidia in *Basidiomycetes*. *New Phytologist* 46(2): 195–228. <https://doi.org/10.1111/j.1469-8137.1947.tb05079.x>
- Corner EJH. 1950. A monograph of *Clavaria* and allied genera. *Annals of Botany Memoirs* 1. 740 p.
- Corner EJH. 1953. Addenda *Clavariaceae*. III. *Annals of Botany*, N.S. 17(2): 347–368. <https://doi.org/10.1093/oxfordjournals.aob.a083355>
- Corner EJH. 1966. Clavarioid genera and *Thelephora* from the Congo. *Bulletin du Jardin Botanique de l'État à Bruxelles* 36(3): 257–279. <https://doi.org/10.2307/3667188>
- Corner EJH. 1970. Supplement to “A monograph of *Clavaria* and allied genera.” *Beihefte zur Nova Hedwigia* 33. 299 p.
- Darriba D, Taboada GL, Doallo R, Posada D. 2012. jModelTest 2: more models, new heuristics and parallel computing. *Nature Methods* 9(8): 772. <https://doi.org/10.1038/nmeth.2109>
- Desjardin DE, Perry BA. 2015. A new species of *Scytinopogon* from the island of Príncipe, Republic of São Tomé and Príncipe, West Africa. *Mycosphere* 6(4): 433–440. <https://doi.org/10.5943/mycosphere/6/4/5>
- Dutta AK, Pradhan P, Roy A, Acharya K. 2012. *Agaricales* of West Bengal, India. I. *Clavariaceae: Clavaria* and *Scytinopogon*. *Indian Journal of Applied and Pure Biology* 27(1): 53–58.
- García-Sandoval R, Cifuentes J, Villegas M. 2004. First record of *Scytinopogon* from Mexico, with notes on its systematics. *Mycotaxon* 89: 185–192.
- Guindon S, Gascuel O. 2003. A simple, fast and accurate method to estimate large phylogenies by maximum-likelihood. *Systematic Biology* 52: 696–704. <https://doi.org/10.1080/10635150390235520>
- Hibbett DS, Binder M, Bischoff JF, Blackwell M, Cannon PF, Eriksson OE & al. 2007. A higher-level phylogenetic classification of the fungi. *Mycological Research* 111: 509–547. <https://doi.org/10.1016/j.mycres.2007.03.004>
- Jülich W. 1981. Higher taxa of *Basidiomycetes*. *Bibliotheca Mycologica* 85. 485 p.
- Katoh K, Standley DM. 2013. MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Molecular Biology and Evolution* 30: 772–780. <https://doi.org/10.1093/molbev/mst010>

- Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, & al. 2012. Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. *Bioinformatics* 28: 1647–1649.
<https://doi.org/10.1093/bioinformatics/bts199>
- Kornerup A, Wanscher JH. 1978. *Methuen Handbook of Colour*. 3rd ed. Eyre Methuen, London. 243 p.
- Largent DL, Johnson D, Watling R. 1977. How to identify mushrooms to genus III: microscopic features. 3rd ed. Mad River Press Inc., Eureka. 148 p.
- Larsson K-H, Læssøe T, Yorou NS, Ryvarden L. 2011. The phylogenetic position of *Hydnodon* and *Scytinopogon*. Abstracts, Mycological Society of American Meeting, Fairbanks, Alaska, 2–5 Aug 2011.
- Meijer AAR de. 2006. Preliminary list of the macromycetes from the Brazilian state of Paraná. *Boletim do Museu Botânico Municipal* 68: 1–55.
- Meijer AAR de. 2008. Notable macrofungi from Brazil's Paraná pine forests. Colombo, PR: Embrapa Florestas. 431 p.
- Meiras-Ottoni A, Gibertoni TB, Larsson K-H. 2021. Additions to *Trechispora* and the status of *Scytinopogon* (*Trechisporales*, *Basidiomycota*). *Mycological Progress* 20: 203–222.
<https://doi.org/10.1007/s11557-021-01667-y>
- Miller MA, Pfeiffer W, Schwartz T. 2010. Creating the CIPRES science gateway for inference of large phylogenetic trees. 1–8, in: *Proceedings of the Gateway Computing Environments Workshop (GCE)*. New Orleans, Louisiana. <https://doi.org/10.1109/GCE.2010.5676129>
- Müller K. 2005. SeqState - primer design and sequence statistics for phylogenetic DNA datasets. *Applied Bioinformatics* 4: 65–69. <https://doi.org/10.2165/00822942-200504010-00008>
- Patouillard. 1907. Basidiomycètes nouveaux du Brésil recueillis par F. Noack. *Annales Mycologici* 5(4): 364–366.
- Petersen RH. 1984. Type studies in the clavarioid fungi. VIII. *Persoonia* 12(3): 225–237.
- Petersen RH. 1988. Notes on clavarioid fungi. XXII. Three interesting South American collections. *Mycologia* 80: 571–576. <https://doi.org/10.1080/00275514.1988.12025581>
- Rambaut A, Suchard MA, Xie D, Drummond AJ. 2014. Tracer v1.6, U.K. Available at: <http://beast.bio.ed.ac.uk/Tracer> (Accessed 10 May 2017).
- Ramírez-Lopes I, Villegas-Ríos M, Cano-Santana Z. 2012. Diversidad de *Agaricomycetes* clavarioides en la Estación de Biología de Chamelas, Jalisco, México. *Revista Mexicana de Biodiversidad* 83: 1084–1095. <https://doi.org/10.22201/ib.20078706e.2012.4.1271>
- Reid DA. 1962. Notes on fungi which have been referred to the *Thelephoraceae* sensu lato. *Persoonia* 2(2): 109–170.
- Rick JE. 1931. *Clavaria robusta* Rick. *Egatea* 16: 120.
- Rick JE. 1959. *Basidiomycetes* Eubasidii in Rio Grande do Sul - Brasília. III. *Iheringia Botânica* 5: 126–192.
- Ronquist F, Huelsenbeck JP. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572–1574. <https://doi.org/10.1093/bioinformatics/btg180>
- Sambrook J, Fritsch EF, Maniatis T. 1989. *Molecular cloning – laboratory manual*, 2nd. Cold Spring Harbor Laboratory Press, New York.
- Sayers EW, Barrett T, Benson DA, Bryant SH, Canese K, Chetvernin V & al. 2009. Database resources of the National Center for Biotechnology Information. *Nucleic Acids Research* 37: D5–D15. <https://doi.org/10.1093/nar/gkn741>
- Simmons MP, Ochoterena H. 2000. Gaps as characters in sequence-based phylogenetic analyses. *Systematic Biology* 49: 369–381. <https://doi.org/10.1093/sysbio/49.2.369>

- Singer R. 1945. New genera of fungi. II. *Lloydia* 8(2): 139–144.
- Stamatakis A. 2014. RAxML Version 8: A tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* 30(9): 1312–1313.
<https://doi.org/10.1093/bioinformatics/btu033>
- Tamura K, Stecher G, Peterson D, Filipski A, Kumar S. 2013. MEGA6: Molecular evolutionary genetics analysis version 6.0. *Molecular Biology and Evolution* 30: 2725–2729.
<https://doi.org/10.1093/molbev/mst197>
- Thiers B. 2017 [continuously updated]. Index Herbariorum: a global directory of public herbaria and associated staff. New York Botanical Garden's Virtual Herbarium.
<http://sweetgum.nybg.org/ih/>. Accessed 23 Apr 2017.
- Thind KS. 1961. The *Clavariaceae* of India. Indian Council of Agricultural Research, New Delhi. 197 p.
- Vellinga EC, Noordeloos ME. 2001. Glossary. 6–11, in: ME Noordeloos ME & al. (eds): *Flora Agaricina Neerlandica*, Vol. 5. A.A. Balkema Publishers, Lisse/Abington/Exton/Tokyo.